1964

Wood Anatomy of Vernonieae (Compositae)

Sherwin Carlquist

Claremont Graduate School

Follow this and additional works at: <https://scholarship.claremont.edu/aliso>

Part of the [Botany Commons](#)

Recommended Citation

Carlquist, Sherwin (1964) "Wood Anatomy of Vernonieae (Compositae)," *Aliso: A Journal of Systematic and Floristic Botany*. Vol. 5: Iss. 4, Article 5.

Available at: <https://scholarship.claremont.edu/aliso/vol5/iss4/5>

WOOD ANATOMY OF VERNONIEAE (COMPOSITAE)

SHERWIN CARLQUIST¹*Claremont Graduate School, Claremont, California*

INTRODUCTION

Although recent workers have emphasized primitive characteristics in various tribes of Compositae, Vernonieae has been regarded as having many features best interpreted as primitive. This is reflected in the comments of Bentham (1873) and in the fact that Hoffmann (1889-1894) placed Vernonieae at the beginning of his treatment of the family. Moreover, Augier and du Merac (1951) regarded Vernonieae as most nearly approximating the primitive stock of the family. The features emphasized by these writers cannot be disregarded, and invite comparison with data from wood anatomy.

The tribe Vernonieae is not a large one, although the genus *Vernonia* itself is one of the larger genera of Compositae. *Vernonia*, which has been broken into many sections, occurs both in the New World and in the Old, and consists of herbs, shrubs, and true trees. Many shrubby and arboreal Vernonias are weedy, and Record and Hess (1943) point out that they tend to occur in clearings. Sources of Old-World Vernonias included in the present study are as follows: *V. arborea* (Java); *V. bockiana* (China); *V. colorata* (Ghana); *V. conferta* (Ghana) and *V. vidalii* (Philippines). Sources of the New-World specimens of *Vernonia* are: *V. baccharoides* (Peru); *V. deppeana* (Costa Rica); *V. leiocarpa* (Costa Rica); *V. menthaefolia* (Cuba); *V. patens* (S. Mexico; Ecuador); *V. salviniae* (Central America); *V. stellaris* (Central America); *V. trichotoma* (Colombia); and *V. triflosculosa* (Costa Rica).

Lychnophora is a small genus (17-20 ssp.) of shrubs and small trees native to Brazil. *Oliganthes* consists of shrubs and trees, and extends from Mexico to Northern Brazil and Peru. The genus *Piptocarpha* comprises about 30 spp. of trees and shrubs, most of which occur in Brazil; the remainder are native to adjacent parts of tropical America. *Vanillosmopsis* contains about seven spp. of Brazilian trees or shrubs. *Proteopsis*, a monotypic Brazilian genus, is a peculiar large-leaved rosette-shrub or herb. This habit is approached in some species of *Lychnophora*.

Little work has been published on wood anatomy of Vernonieae. Metcalfe and Chalk (1950) mention certain features in the genera (species not cited) *Lychnophora*, *Piptocarpha*, and *Vernonia*. Lecomte (1922) offers some information on the wood of *Apodoccephala pauciflora*. Other species considered by Lecomte as belonging to *Vernonia* were treated earlier (Carlquist, 1961) under the genus *Brachylaena*, which most authors consider as belonging to Inuleae, although it may be close to Vernonieae.

MATERIALS, METHODS AND ACKNOWLEDGMENTS

Wood samples from the Samuel J. Record Collection of Yale University were generously made available by Dr. William L. Stern, formerly of that institution. These samples formed

¹This research was supported by a National Science Foundation Grant, NSFG-5428, which is permitting completion of studies on wood anatomy of Compositae and related families. Publication was financed by a similar grant, NSFG-23396.

the nucleus for the present study. Additional wood samples from the wood collection of the Arnold Arboretum, Harvard University, were provided through the kindness of Dr. I. W. Bailey. Wood samples are cited in table 1 with abbreviations according to those offered by Stern and Chambers (1960). Herbarium specimens, where known, are cited in accordance with the abbreviations given by Lanjouw and Stafleu (1959). A set of duplicate wood slides representing the species employed in this study has been deposited at the Division of Woods, Smithsonian Institution, Washington, D. C. The assistance of Mr. Alfred G. Diboll, Mr. Charles F. Quibell, and Mr. Loran Anderson, who sectioned the woods studied, is gratefully acknowledged. The methods used in sectioning are the same as those outlined earlier (Carlquist, 1958).

ANATOMICAL DESCRIPTIONS

Table 1 is a summary of qualitative and quantitative features of Vernonieae, similar to those cited in earlier papers on wood anatomy of tribes of Compositae. Characteristics which cannot be summarized conveniently in chart form are discussed in the text under appropriate headings. Absence of figures for uniseriate rays indicate that few or no such rays were present, and measurements would be meaningless.

Explanation of symbols in table 1:

- cg = grooves interconnecting many pits
in a helix
- fb = fine bands on vessel walls
- ff = a few fibers
- g = grooves interconnecting two or several
pits in a helix on a vessel wall
- mv = more numerous vessels in early wood
- p = axial parenchyma
- wv = wider vessels in early wood
- + = presence of characteristic
- 0 = absence of characteristic
- = presence of characteristic to a limited
extent

VESSEL ELEMENTS

Dimensions, Shapes, Types.—In contrast with other tribes of Compositae, short vessel elements are unusual in Vernonieae, and only in the genus *Lychnophora* does the average length of vessel elements fall below 200 μ . Exceptionally long vessel elements for the family characterize a number of Vernonieae. Species with elements averaging over 400 μ in length include *Piptocarpha macropoda* (fig. 8), *Vernonia arborea* (fig. 18), *V. conferta* (fig. 20), *V. trichotoma*, and especially *V. salvinae* (fig. 16), which has the longest vessel elements yet reported for the family. The possible significance of the long, narrow elements in *V. salvinae* is discussed later. The lack of exceptionally short vessel elements in Vernonieae must be considered a lack of great specialization. Relatively a large proportion of the tribe, however, possesses wide vessel elements. Species in which the average diameter exceeded 100 μ include *Oliganthes discolor* (fig. 5, 6), *Piptocarpha macropoda* (fig. 7), *Vernonia arborea* (fig. 17), *V. baccharoides* (fig. 13, 14), *V. colorata*, *V. conferta*, *V.*

deppeana, *V. patens*, *V. stellaris*, and *V. vidalii*. Exceptionally narrow vessel elements are unusual, and the figures in table 1 show only a relatively few species in which the average diameter is less than $65\ \mu$. The lack of extremely narrow vessel elements may help to account for the fact that in contrast with other tribes of Compositae, such as Astereae (Carlquist, 1960), vascular tracheids were not observed in any Vernoniaceae. Lack of extremely narrow, short vessel elements is probably related to the comparatively mesic, tropical environments in which most Vernoniaceae grow. Certainly none of the Vernoniaceae studied could be said to grow in an arid environment.

Caudate vessel elements are not especially conspicuous in Vernoniaceae. However, the markedly long vessel elements of *Vernonia salvinae* (fig. 16) are mostly caudate.

As in most other groups of Compositae, perforation plates are almost exclusively simple. As in other tribes, however, a few Vernoniaceae do have multiperforate plates in which many (10–20) bars are present. These bars are occasionally forked and otherwise misshapen, but most often form a nearly scalariform pattern. Species possessing such plates include *Lychnophora affinis* (fig. 3), *Oliganthes acuminata*, *O. discolor*, *Vernonia trichotoma*, and *V. triflosculosa*. Multiperforate plates were reported for the genus *Lychnophora* by Metcalfe and Chalk (1950). They are probably present in a wider variety of Vernoniaceae than listed above, and are easily overlooked in examining sections. The phylogenetic significance of these occasional multiperforate plates in a family with characteristically simple plates is not clear. However, their relative abundance in Vernoniaceae might be related to the rather low level of specialization (for Compositae) which vernonioid woods exhibit.

Lateral-Wall Pitting.—Alternate circular bordered pits, averaging between $4\ \mu$ and $6\ \mu$ in diameter, characterize most Vernoniaceae. Larger pits were observed in *Vernonia conferta* (fig. 21), *V. deppeana* (fig. 24), *V. menthaefolia* (fig. 19), *V. patens*, and *V. stellaris*. Exceptionally small pits, on the contrary, occur in the three species of *Lychnophora* (fig. 3), *Oliganthes* and *Vanillosmopsis* (fig. 27), as well as in certain Vernonias, including *V. bockiana* (fig. 25), *V. colorata*, *V. leiocarpa*, *V. triflosculosa*, and *V. vidalii* (fig. 26). Exceptionally small pits of this nature are not common in Compositae, but have been reported in a number of Inuleae (Carlquist, 1961). Although elliptical apertures on intervascular pits characterize most Compositae, circular apertures were seen on some pits in Vernoniaceae, such as those of *Vernonia deppeana* (fig. 24). Many of the species with relatively large pits showed pit cavities which, in face view, exhibited mutual compression, forming a honeycomb-like pattern, like that shown earlier for *Hymenoclea salsola* (Carlquist, 1958, fig. 31) or *Pluchea scabrida* (Carlquist, 1961, fig. 5).

Occasionally in Vernoniaceae intervascular pits are elongate in shape, forming a near-scalariform pattern. This is shown for *Vernonia conferta* in fig. 22. Such scalariform-like pitting, however, is common in vessel-parenchyma pitting in some species of Vernoniaceae. Often, this pitting consists of pits much larger in size than the intervascular ones, and with very wide apertures. Comparison of fig. 21 and 23, or fig. 28 and 29, shows this clearly for *Vernonia conferta* and *V. baccharoides*, respectively. Other species in which vessel-parenchyma pitting was clearly different from intervascular pitting in such respects include *Vernonia menthaefolia*, *V. patens*, and *V. deppeana*. In the last-named species, vessel-parenchyma pits possess vestigial borders or none at all, much like those illustrated for *V. baccharoides* in fig. 29.

Helical Sculpture.—Various forms of helical sculpture are abundant in certain tribes of Compositae, and have been discussed in detail earlier (Carlquist, 1957, 1958, 1960). The most prominent types of bands are not present in Vernoniaceae. However, simple grooves interconnecting two or more pit apertures in a helix are present in some species (denoted by

TABLE 1. *Wood Characteristics of Vernoniae.*

SPECIES	COLLECTION	DIAMETER WIDEST VESSEL, μ	DIAMETER VESSELS, AVERAGE, μ
<i>Lychnophora affinis</i> Gard.	Barreto 192, Yw-42605	110	67.0
<i>Lychnophora brunoides</i> Mart.	Assis 5739 (GH)	86	45.9
<i>Lychnophora tomentosa</i> (Mart.) Sch. Bip.	Barreto 187, Yw-42603	97	45.6
<i>Oliganthes acuminata</i> DC.	Pittier 14113, Yw-34288	108	63.0
<i>Oliganthes discolor</i> (Kunth) Sch. Bip.	Yw-18353	118	83.7
<i>Oliganthes discolor</i> (Kunth) Sch. Bip.	Ducke 315 (Y), Yw-34079	151	117.7
<i>Oliganthes hypochlora</i> Blake	Williams 10348 (F), Yw-36313	108	66.7
<i>Oliganthes karstenii</i> Sch. Bip.	Williams (F), Yw-17629	140	102.6
<i>Piptocarpha axillaris</i> Baker	Yw-23892	106	57.7
<i>Piptocarpha macropoda</i> (DC.) Baker	Bot. Gard. São Paulo 38, Yw-42614	192	119.9
<i>Piptocarpha sodiroi</i> Hieron.	Rimbach 835 (Y), Yw-34186	119	75.6
<i>Proteopsis sellowii</i> Sch. Bip.	Mexia 5872 (UC)	65	45.3
<i>Vanillosmopsis erythropappa</i> (DC.) Sch. Bip.	Barreto 193, Yw-42606	119	75.0
<i>Vernonia arborea</i> Buch.-Ham.	Krukoff 4146, Aw-20202	281	205.6
<i>Vernonia arborea</i> f. <i>glabra</i> Koord. & Jalet	Yw-31134	205	166.0
<i>Vernonia baccharoides</i> Kunth	Williams 2046 (F), Yw-2046	162	93.9
<i>Vernonia baccharoides</i> Kunth	Williams 3967 (F)	183	117.5
<i>Vernonia baccharoides</i> Kunth	Yw-17597	183	130.7
<i>Vernonia baccharoides</i> Kunth	William 1476 (F)	194	100.6
<i>Vernonia bockiana</i> Diels	Tang 221, Yw-21833	151	79.5
<i>Vernonia colorata</i> Drake	Vigne 2904, Yw-24008	173	109.6
<i>Vernonia conferta</i> Blake	Vigne 2435, Yw-23236	184	108.0
<i>Vernonia deppeana</i> Less.	Edwards 5 (A), Aw-20203	205	136.8
<i>Vernonia leiocarpa</i> DC.	Edwards 168 (A), Aw-20201	108	65.9
<i>Vernonia methaefolia</i> Less.	Jack 4875 (A), Aw-20200	173	88.6
<i>Vernonia patens</i> Kunth	Williams 9024 (F), Yw-24762	170	79.1
<i>Vernonia patens</i> Kunth	Acosta-Solis 6406, Yw-45168	184	121.0
<i>Vernonia patens</i> Kunth	Williams 9116 (F)	173	110.1
<i>Vernonia salvinae</i> Hemsl.	Skutch 953 (A), Aw-22946	86	65.1
<i>Vernonia stellaris</i> Llav.	I. Bailey 2, Aw-27289	205	112.9
<i>Vernonia trichotoma</i> Gleason	Cuatrecasas 20796, Yw-44453	120	87.4
<i>Vernonia triflosculosa</i> Kunth	Stork 4124 (Y), Yw-38344	108	73.2
<i>Vernonia vidalii</i> Merr.	Yw-2239	190	146.7

VESSELS PER GROUP, AVERAGE	LENGTH VESSEL ELEMENTS, AVERAGE, μ	LENGTH LIBRIFORM FIBERS, AVERAGE, μ	MAXIMUM WIDTH LIBRIFORM FIBERS, AVERAGE, μ	WALL THICKNESS FIBERS, μ	PIT DIAMETER, μ	HELICAL SCULPTURE ON VESSELS	ELEMENTS DISTINGUISHING RINGS	STORIED ELEMENTS	HEIGHT MULTISERiate RAYS, AVERAGE, mm	HEIGHT UNISERiate RAYS AVERAGE, μ	MAXIMUM WIDTH MULTISERiate RAYS, CELLS, AVERAGE	RAY CELLS ISODIAMETRIC TO PROCUMBENT	RAY CELLS ISODIAMETRIC TO ERECT
2.80	186	416	12.7	6	2-3	cg, fb	p, vv	0	.18	57	2.20	+	-
2.85	164	378	17.5	6	2-3	cg, fb	p, vv	0	.25	94	2.18	+	-
4.22	232	448	29.7	6-12	3-4	cg	p, vv	0	.28	90	2.88	+	-
2.12	253	386	13.2	3	2	cg, fb	wv	0	.16	59	2.60	+	-
1.41	255	497	21.6	2-3	2	cg, fb	0	0	.18	68	2.48	+	0
1.64	338	543	28.5	2-3	3	cg, fb	0	0	.29	87	3.22	+	0
1.85	321	564	15.7	3	2	cg, fb	p, vv	0	.23	92	2.48	+	-
1.90	362	624	29.3	2	3	cg, fb	0	0	.28	153	3.60	+	-
1.44	295	367	19.4	3-4	4-5	cg, fb	p, vv	0	.26	73	3.26	+	-
1.55	403	648	25.8	3-4	5	0	p, vv	0	.51	134	3.50	+	-
1.30	306	456	16.4	4	2-3	cg, fb	0	0	.47	143	3.67	+	-
3.23	221	356	20.0	7	4	0	0	0	.26	106	2.46	+	-
1.79	315	518	19.2	4	3	cg, fb	p, vv	0	.17	123	2.05	+	0
1.63	497	877	40.2	2-3	4	g, cg	0	0	.78	243	3.65	+	-
1.10	398	684	38.2	2-3	4	g, cg	0	ff	.68	160	5.20	+	-
1.67	236	592	25.2	3-4	5-6	g	wv	0	.94		6.24	-	+
1.53	266	413	28.9	4-5	4-5	g	mv	ff	1.83		8.10	-	+
1.89	380	620	31.0	3-4	6	0	0	0	3.13		7.77	+	+
1.60	223	392	27.2	3-4	5-7	g	p, vv	ff	1.55		7.87	+	+
1.79	270	382	24.2	4-7	3	cg, fb	wv	ff	.63		4.09	+	+
1.48	240	372	22.2	3-4	3	cg, fb	p, vv	0	.59	192	3.90	+	+
1.94	392	680	31.3	3-4	6-7	0	0	0	2.32		11.70	+	-
1.56	420	566	33.5	3-5	8-9	0	0	0	1.82	173	4.50	+	+
2.00	326	594	27.7	6-9	3	cg, fb	0	0	.50	176	3.13	+	+
2.11	307	476	25.7	5	7-8	0	mv	0	2.15		5.78	+	+
1.68	314	629	32.8	3-4	6-8	0	p, mv	0	.82		12.50	+	+
1.69	357	603	31.2	3-4	6-8	0	0	0	1.29		7.50	+	+
1.77	282	761	28.8	4-5	6-8	0	p, mv	0	1.22		10.17	+	+
1.19	643	1091	31.5	3-5	5	0	0	0	>3		5.12	0	+
1.75	323	781	30.8	3-4	7-8	0	0	0	1.11		7.04	+	+
1.71	513	712	38.8	4-5	3-4	g	0	0	2.67	155	5.12	+	+
1.68	231	518	29.5	4-5	2-3	cg, fb	0	0	.60	113	5.88	+	-
1.38	348	751	35.5	2-3	3	cg, fb	0	0	.40	177	4.12	+	-

"g" in table 1). Continuous grooves ("cg"), interconnecting a larger number of pit apertures, are even more common. These continuous grooves are almost always accompanied by a pair of fine bands. Good examples of grooves may be seen in fig. 25–27. These figures do not suggest the presence of fine bands, which are difficult to photograph. Table 1 lists the species in which continuous grooves, accompanied by fine bands, occur. In two species, *Piptocarpha macropoda* and *Vernonia menthaefolia*, helical sculpture could not be said to be present, but pit apertures are very wide at the inner surface of a vessel, and thus almost form grooves interconnecting with similarly wide pits of adjacent pits.

The significance of helical sculpture in these Vernonieae is not readily apparent, but might be related to a modest degree of aridity (e.g., a dry season, at least). Helical sculpture of Vernonieae is not nearly so pronounced as it is in Compositae which occur in desert regions, such as many Astereae (Carlquist, 1960). The presence of the relatively minute grooves and bands in Vernonieae cannot be considered a marked specialization, but they are reminiscent of the expressions of helical sculpture found in certain Inuleae (Carlquist, 1961).

Vessel Grouping.—Vernonieae are notable in the small degree to which vessels are grouped. Although the figure for vessel grouping is relatively high in *Lychnophora* (fig. 1) and *Proteopsis*, extensive vessel groups are not present even in these genera.

LIBRIFORM FIBERS

Figures for average length, average width (at the widest point) and wall thickness of libriform fibers are given in table 1. The figures for length yield no surprises and correlate well with vessel-element lengths for the species studied. Notably wide fibers occur in *Vernonia arborea* (fig. 17) and *Vernonia trichotoma*. Thick-walled fibers, in which the lumen is very nearly occluded, characterize the genera *Lychnophora* (fig. 1, 2), *Proteopsis*, and *Vanillosmopsis* (fig. 9, 10). Thick-walled fibers occur in some species of *Vernonia*, such as *V. bockiana* and *V. leiocarpa*. Other species of *Vernonia* have relatively thin-walled fibers. Extremely thin-walled fibers are seen in *V. arborea* (fig. 17), and *V. vidalii*.

Septate fibers, which were reported by Metcalfe and Chalk (1950), were observed in most of the species of *Vernonia* included in the present study, such as *V. bockiana*, *V. conferta* (fig. 20), *V. deppeana*, *V. menthaefolia* (fig. 15), *V. patens*, *V. salvinae*, *V. stellaris*, and *V. trichotoma*. One to three septa characterize fibers of *V. baccharoides*.

AXIAL PARENCHYMA

Apotracheal Parenchyma.—As noted in table 1 under the column headed "elements distinguishing rings," parenchyma cells, which are referable to the concept of fiber dimorphism developed earlier by the writer (1958), occur in the early wood of some species. Narrow bands are shown here for *Lychnophora tomentosa* (fig. 1). Very wide apotracheal parenchyma bands may be seen in *Piptocarpha macropoda* (fig. 7) and *Vernonia bockiana* (fig. 11).

Vasicentric Parenchyma.—Like all Compositae, Vernonieae may be said to have scanty vasicentric parenchyma. In some, however, such as *Vernonia bockiana* and *V. vidalii*, parenchyma forms a complete sheath around vessels and vessel groups. Vasicentric paren-

Fig. 1–4. Fig. 1–3. *Lychnophora tomentosa*.—Fig. 1. Transection. Three narrow bands, running horizontally across the section, may be seen.—Fig. 2. Tangential section. Note narrow multiseriate rays, abundance of uniseriate rays.—Fig. 3. Portion of radial section, showing two nearly-scalariform perforation plates.—Fig. 4. *Lychnophora affinis*. Radial section, showing sclerified tyloses. Dark areas contain resin-like deposits. Fig. 1, 2, 4, $\times 70$; fig. 3, $\times 500$.

FIGURES 1-4

chyma is especially thick (up to three or four cells) around vessels and vessel groups in *Vernonia arborea* (fig. 17) and *V. colorata*.

Ordinarily, vasicentric parenchyma occurs in strands of one to three cells. Four to eight cells may constitute a strand in *Vernonia stellaris*, however.

VASCULAR RAYS

The Vernonieae other than *Vernonia* studied here are notable in that uniseriate rays are relatively abundant. Although uniseriates are never as frequent as multiseriate rays, they are frequent in all of those genera, as shown by *Lychnophora tomentosa* (fig. 2), *Oliganthes discolor* (fig. 6), *Piptocarpha macropoda* (fig. 8) and *Vanillosmopsis erythropappa* (fig. 10). In *Vernonia*, they show various degrees of elimination. Uniseriates are abundant in *V. leiocarpa* and *V. vidalii*. They are far less frequent in *V. arborea*, and few are present in *V. bockiana*, *V. colorata*, *V. deppeana*, and *V. trichotoma*. In the remaining species of *Vernonia* studied, they are so infrequent as to be negligible.

Multiseriate rays are very low and narrow in *Lychnophora* (fig. 2), *Oliganthes* (fig. 6), *Piptocarpha* (fig. 8), *Proteopsis*, and *Vanillosmopsis* (fig. 10). In contrast, rays are notably wide in *Vernonia baccharoides*, (fig. 12), *V. conferta* (fig. 20), *V. menthaefolia* (fig. 15), *V. patens*, *V. stellaris*, and *V. triflosculosa*. Multiseriate rays are exceptionally high in *V. baccharoides*, *V. conferta*, *V. leiocarpa*, *V. menthaefolia* (fig. 15), *V. patens*, *V. salvinae*, (fig. 16), *V. stellaris*, and *V. trichotoma*. Wings on multiseriate rays of Vernonieae are mostly one cell in extent.

With regard to histology, Vernonieae are distinctive in the presence of multiseriate rays in which procumbent cells are abundant. In table 1, presence of both procumbent and erect cells is indicated. If both are indicated to be present, multiseriate rays may be said to possess a central region of procumbent cells, with a sheath (usually one cell layer) of erect cells, and erect cells present as wings on the ray. If erect cells are indicated as present to a limited extent, they are restricted mostly to wings of the rays. In a few cases (*Oliganthes discolor*, *Vanillosmopsis erythropappa*) virtually no erect cells were observed. A tendency toward uniform procumbency of ray cells is thus present in a few species. However, the reverse tendency, predominance of erect cells, was observed only in *Vernonia baccharoides*, *V. salvinae*, and *V. stellaris*. This situation is curious because of the great number of Compositae in which erect cells are abundant or predominant, sometimes exclusively so. This is, for example, true of many Heliantheae (Carlquist, 1958).

Ray cells of the Vernonieae studied are all relatively thin-walled, but have secondary walls which are lignified. The only exception to this was observed in *Vernonia menthaefolia*, in which ray cells at the beginning of growth rings were observed to have non-lignified walls.

As observed earlier by Chalk and Chattaway (1933), perforated ray cells appear to occur in species which have relatively wide rays in which ontogenetic breakup of rays is occurring actively. In Vernonieae, perforated ray cells may be found in species of this nature, such as *Vernonia patens*.

TYLOSES

Both thin-walled and thick-walled tyloses were observed in *Vernonia baccharoides*. Thin-walled tyloses may be seen in the photograph, fig. 13. Thick-walled, lignified tyloses were

Fig. 5-8. Fig. 5-6. *Oliganthes discolor*.—Fig. 5. Transection.—Fig. 6. Tangential section. Note low rays.—Fig. 7-8. *Piptocarpha macropoda*.—Fig. 7. Transection. Note zones of parenchyma (e.g., center right).—Fig. 8. Tangential section. Rays are relatively high, mostly multiseriate. All, $\times 70$.

FIGURES 5-8

abundant in the material of *Lychnophora affinis* examined (fig. 4). Thick-walled tyloses of this nature are infrequent in Compositae, but have been observed in several species of *Fitchia* (Carlquist, 1958; Carlquist and Grant, 1963). Thin-walled tyloses were observed in *Vernonia menthaefolia*.

GROWTH RINGS

Growth-ring phenomena are not markedly pronounced in Vernonieae, and very few could be said to have a ring-porous tendency. The elements distinguishing early wood of growth rings, as indicated in table 1, do not differ markedly from those of late wood. Growth-ring phenomena of this sort are shown in fig. 1 and 13.

STORIED WOOD STRUCTURE

As indicated in table 1, a few species of Vernonieae possess a modest, almost imperceptible degree of storying in which a few fibers in certain areas of a section are storied. This may be seen in fig. 18 (upper right). Vernonieae are relatively unusual among Compositae in the modest degree of storying present, for other tribes possess not only a higher proportion of species with storied structure, but also may have a more marked expression of storying in any given species.

RESINOUS DEPOSITS

All of the species of Vernonieae studied possess droplets of resin-like materials, in varying degrees, in both axial and ray parenchyma cells. Droplets in fibers were also observed in *Vanillosmopsis erythropappa*, *Vernonia patens*, and *V. trichotoma*. Massive deposits of the resin-like materials were observed in vessels of *Lychnophora affinis* (fig. 4; note also in rays), *Oliganthus acuminata*, *O. karstenii*, *Piptocarpha axillaris*, *P. sodiroi*, *Proteopsis sellowii*, *Vanillosmopsis erythropappa*, *Vernonia baccharoides*, *V. salvinae*, *V. stellaris*, and *V. trichotoma*. Massive deposits of resinous materials also occur in rays of *V. patens* and *V. trichotoma*. A curious feature observed in *Vanillosmopsis erythropappa* is the occurrence of resinous deposits, which had become carbonized, in intercellular spaces among groups of fibers. Deposits of these materials are thus relatively abundant in Vernonieae, for a number of Compositae lack them altogether in secondary xylem.

CRYSTALS

Crystals are relatively unusual in Compositae, although they have been reported in *Proustia*, of Mutisieae (Metcalf and Chalk, 1950) and certain Astereae (Carlquist, 1960). Prominent prismatic and rhomboidal crystals occur in Vernonieae in rays of *Vernonia menthaefolia* (fig. 19). In *V. stellaris*, small prismatic and druse-like aggregations of crystals were observed in rays. In *V. baccharoides* (Yw-17597 only) small druses were observed in ray cells.

TAXONOMIC AND PHYLOGENETIC CONCLUSIONS

SPECIES CHARACTERISTICS

In the genus *Piptocarpha*, *P. macropoda* is distinctive in its wide bands of apotracheal parenchyma, the lack of helical sculpture on vessel walls, and the long, wide vessel elements.

Fig. 9-12. Fig. 9-10. *Vanillosmopsis erythropappa*.—Fig. 9. Transection. Massive deposits of resin-like materials may be seen in some vessels.—Fig. 10. Tangential section. Rays are limited in vertical height, uniseriatae are abundant.—Fig. 11-12. *Vernonia bockiana*.—Fig. 11. Transection. Abundance of parenchyma characterizes this wood.—Fig. 12. Tangential section. Note abundance of multiseriate rays. All, $\times 70$.

FIGURES 9-12

Because only a small segment of the genus *Vernonia* has been studied here, species characteristics in secondary xylem are difficult to estimate. Certainly the extremely high rays, lacking in procumbent cells, and the long, narrow vessel elements of *Vernonia salvinae* mark that species as highly distinctive. *Vernonia arborea* is marked by its wide, thin-walled fibers and its very wide vessels. Very wide rays (*V. conferta*, fig. 20; *V. patens*) may characterize some species of *Vernonia*, and obviously species of *Vernonia* differ markedly in the average height of rays, and the relative abundance of uniseriate rays.

GENUS CHARACTERISTICS

The genus *Lychnophora* is distinctive in its narrow vessels, with small pits, thick-walled fibers, low, narrow multiseriate rays, abundance of uniseriate rays, and narrow bands of apotracheal parenchyma. *Oliganthes* differs in having wider, longer vessels and thinner-walled fibers. *Proteopsis* resembles *Lychnophora* in a number of xylary features, but differs in lack of sculpture on vessels. The genus *Vernonia* could be compared with other large genera of Compositae, such as *Senecio* or *Baccharis*, and could be contrasted, but this contrast would largely take the form of differing tendencies within the genus, although it is conceivable that certain species might be similar. The tendencies within Vernonieae are discussed below.

PHYLOGENETIC TENDENCIES IN VERNONIEAE

Vernonieae are of especial interest within Compositae in that characters of the secondary xylem present, in the aggregate, rather unspecialized (for Compositae) features. The relatively long, wide vessel elements, without marked tendencies toward narrowness and shortness, can be cited in this regard. Vascular tracheids are absent. Helical sculpture is not markedly specialized. Vessel grouping is minimal. Storying is rare, and expressed only in a rudimentary way. Rays are relatively unspecialized in most taxa, which have a type corresponding to Kribs' (1935) Heterogeneous IIB. Abundance of uniseriate rays in most Vernonieae is certainly an unspecialized condition when compared with their infrequency in many species of other tribes.

The great length of vessel elements (compared with Compositae at large) in *Vernonia salvinae* and *V. trichotoma* is probably an indication of paedomorphosis, not primitiveness *per se*, in accordance with the theory propounded by the writer (1962). The high, wide, primary-xylem-like rays in these species are also suggestive of this explanation, and may also help to explain the dimensions of rays in some other Vernonias. In his discussion of paedomorphosis, the writer (1962) suggested that abundance of erect cells in multiseriate rays—characteristic of *Vernonia baccharoides* and *V. salvinae*—may also reflect juvenile tendencies.

The Vernonieae other than *Vernonia* are remarkably uniform in their general construction, and recall unspecialized woods of other tribes, such as *Stenopadus* and *Hesperomannia* of Mutisieae (Carlquist, 1957), or *Perymenium* and *Verbesina* of Heliantheae (Carlquist, 1958). Within the genus *Vernonia* specialization may include extreme wideness of vessels (many *Vernonia* spp.), very thin-walled fibers (*V. arborea*, *V. vidalii*), elimination of uniseriate rays, presence of storying in libriform fibers, and possibly changes in ray dimensions and histology.

Fig. 13–16. Fig. 13–14. *Vernonia baccharoides*, Williams 1476.—Fig. 13. Transection. The end of a growth ring is seen, above.—Fig. 14. Tangential section, illustrating wide, short vessels and wide, high multiseriate rays.—Fig. 15. *Vernonia menthaefolia*. Tangential section. Rays are extremely tall.—Fig. 16. *Vernonia salvinae*. Vessel elements are very long; rays are tall, narrow. All, $\times 70$.

FIGURES 13-16

Fig. 17-19. Fig. 17-18. *Vernonia arborea* f. *glabra*, Yw-31134.—Fig. 17. Transection. Band of very thin-walled fibers may be seen, above; note large diameter of vessels.—Fig. 18. Tangential section. Parenchyma, center; a number of fibers form a somewhat storied pattern.—Fig. 19. *Vernonia menthaefolia*. Portion of tangential section. Intervascular pits are round, with apertures of some interconnected by grooves. Rays contain crystals, which are square to rhomboidal in outline. Fig. 17, 18, $\times 70$. Fig. 19, $\times 280$.

As noted earlier (Carlquist, 1961), certain Inuleae show considerable similarity to Vernoniaceae. Such similarities include small size of pits, narrow, relatively low rays, grooving in vessels, and relatively thick-walled fibers (*Oliganthus* and *Lychnophora* of Vernoniaceae; *Brachylaena* of Inuleae). Very compelling similarities exist between some Vernoniaceae and

Fig. 20-24. Fig. 20-23. *Vernonia conferta*. Tangential section. Uniseriate rays are absent.—Fig. 21-23. Portions of vessel walls from the same section, showing different types of pitting.—Fig. 21. Intersvascular pitting, showing pits circular in outline, with pit apertures also circular in outline.—Fig. 22. Intersvascular pitting, with transitional or near-scalariform pitting predominant.—Fig. 23. Vessel-parenchyma pitting, showing similar transitional pitting, mostly with somewhat wider apertures than in fig. 22.—Fig. 24. *Vernonia deppeana*. Intersvascular pitting, showing relatively large pits in which both the pit cavities and apertures have a circular outline in face view. Fig. 20, $\times 70$. Fig. 21-24, $\times 500$.

Fig. 25–29. Vessel-wall pitting.—Fig. 25. *Vernonia bockiana*, showing wall partly cut away. The prominent continuous grooves interconnecting pit apertures may be seen.—Fig. 26. *Vernonia vidalii*. Portions of walls of two adjacent vessel elements. Grooves interconnecting apertures may be seen; note that the direction of grooves in element at left runs in a different direction from those of element at right.—Fig. 27. *Vanillosmopsis erythropappa*. Portions of several vessel elements to illustrate minute intervascular pitting and, at right, the continuous grooves.—Fig. 28–29. *Vernonia baccharoides*, Williams 1476.—Fig. 28. Vessel wall showing intervascular pitting, above; a few vessel-parenchyma pits, below, show wide apertures but prominent borders.—Fig. 29. A vessel-wall showing vessel-parenchyma pitting. Note large size, elongate shape of these pits as compared with intervascular pitting. Borders are vestigial or lacking. All, $\times 500$.

some Mutisieae. Individual comparisons (e.g., *Vernonia arborea* of Vernonieae and *Tessaria* of Inuleae) may be striking, but probably reflect parallelisms. Because the gamut of differentiation and specialization in wood anatomy of Compositae is relatively small, little emphasis should be placed on comparisons among large assemblages of Compositae.

Vernonieae exhibit a wide variety of species in which unspecialized (for Compositae) conditions occur, and the relative primitiveness in xylary structure suggests that further investigations into comparative anatomy of other portions of species of Vernonieae would be rewarding. The data from wood anatomy do tend to give a measure of support to those who hold that Vernonieae contain a large number of characteristics primitive within Compositae.

LITERATURE CITED

- Augier, J., and Marie-Louise du Merac. 1951. La phylogénie des Composées. *La Revue Sci.* 89: 167-182.
- Bentham, G. 1873. Notes on the classification, history, and geographical distribution of Compositae. *J. Linn. Soc. Botan.* 13: 335-577.
- Carlquist, S. 1957. Wood anatomy of Mutisieae (Compositae). *Trop. Woods* 106: 29-45.
- . 1958. Wood anatomy of Heliantheae (Compositae). *Trop. Woods* 108: 1-30.
- . 1960. Wood anatomy of Astereae (Compositae). *Trop. Woods* 113: 54-84.
- . 1961. Wood anatomy of Inuleae (Compositae). *Aliso* 5: 21-37.
- . 1962. A theory of paedomorphosis in dicotyledonous woods. *Phytomorphology* 12: 30-45.
- , and M. L. Grant. 1963. Studies in *Fitchia*: novelties from the Society Islands; anatomical studies. *Pacific Science* 17: 282-298.
- Chalk, L., and M. Margaret Chattaway. 1933. Perforated ray cells. *Proc. Roy. Soc. London B* 113: 89-92.
- Hoffman, O. 1889-1894. Compositae. In, Engler & Prantl, *Die natürlichen Pflanzenfamilien* 4(5): 87-391.
- Kribs, D. A. 1935. Salient trends of structural specialization in the wood rays of dicotyledons. *Botan. Gaz.* 96: 547-557.
- Lanjouw, J., and F. Stafleu. 1959. Index herbariorum. Part I. The herbaria of the world. ed. 4. International Bureau for Plant Taxonomy and Nomenclature. Utrecht.
- Lecomte, H. 1922. Les bois de la forêt d'Analamazaotra. Augustin Challonel. Paris.
- Metcalf, C. R., and L. Chalk. 1950. Anatomy of the dicotyledons. Vol. 2. Clarendon Press, Oxford.
- Record, S. J., and R. W. Hess. 1943. Timbers of the New World. Yale University Press, New Haven.
- Stern, W. L., and K. Chambers. 1960. The citation of wood specimens and herbarium vouchers in anatomical research. *Taxon* 9: 7-13.